# A RE-EXAMINATION OF *LITHOSMYLIDIA* RIEK FROM THE TRIASSIC OF QUEENSLAND WITH NOTES ON MESOZOIC 'OSMYLID-LIKE' FOSSIL NEUROPTERA (INSECTA : NEUROPTERA)

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*Lithosmylidia* Riek, a genus of fossil Neuroptera from the Triassic of Queensland, is redescribed. Its three species *L. lineata* Riek, *L. parvula* Riek and *L. baronne* sp. nov., have affinities with the Osmylidae and/or Polystoechotidae. Similar 'osmylid-like' species from elsewhere in the Mesozoic are briefly discussed.

Lithosmylidia, Neuroptera osmylid-like, Triassic, Mesozoic, Queensland.

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Lithosmylidia Riek is a genus of fossil Neuroptera established for two species from the Triassic of Mount Crosby in south-eastern Queensland (27°32'S, 152°48'E) (Riek, 1955). Two new fairly well-preserved specimens of Lithosmylidia, one from Mount Crosby, and the other from Triassic beds near Gayndah in central Queensland (25°37'S, 151°37'E), have prompted this revision and reassessment of Lithosmylidia, as well as a brief review of similar Mesozoic 'osmylid-like' species.

The Mount Crosby fossil insects occur in green shales of the Late Triassic (Karnian) (De Jersey, 1971) Mount Crosby Formation and have been collected at five separate exposures designated as Fossil Insect Localities, A,B,C,D, and E (details in Allen, 1961). Riek (1955) has recorded eight species of Neuroptera in six genera, one of which, *Lithosmylidia*, is the subject of the present study.

The specimen from near Gayndah was collected in grey shales of the Middle Triassic (de Jersey, 1979) Gayndah Beds in a road cutting approximately 3 km ENE of Gayndah. Fossil insects were discovered there in 1962 and recorded in an unpublished Geological Survey of Queensland report (Woods, 1962) which was referred to by Ellis (1968).

The following museum abbreviations are used: QM, Queensland Museum; UQDG, University of Queensland, Department of Geology.

#### Genus Lithosmylidia Riek

Lithosmylidia Riek, 1955, p. 678.

Type species, by original designation, *Lithosmylidia lineata* Riek, 1955.

#### DESCRIPTION

Neuroptera from the Triassic of Queensland, Australia. Forewing: medium to large, over  $2 \times$ as long as wide; trichosors present; subcostal space apparently without crossveins; Sc and  $R_1$ fused apically and thence curved posteriad to enter margin well before wing apex; apparently without  $r_1$ -rs, or with very few (1 only detected in 1 specimen of L. parvula Riek); Rs originating close to base of wing, with at least 10 pectinate branches; basal stem of MA apparently absent; crossveins of Rs-MA field not well preserved in most material, but apparently of limited extent (in the most clearly preserved specimen (QM F14359) restricted to a few random ones proximally and 2 irregular gradate series distally); MP forked near the base; CuA pectinately forked, with branches oblique; CuP dichotomously forked; anal field well developed, extending a considerable distance along posterior margin; 1A long and multibranched. Hindwing and other body parts not known.

#### Notes

On the basis of venational variation in recent Neuroptera, the three species here included in *Lithosmylidia* are probably generically distinct. However, the available incomplete and often indistinctly preserved material does not offer enough information to justify and diagnose separate genera for each. *Lithosmylidia*, as presently defined, should thus be considered as a fairly broadly embracing 'holding' genus until additional material permits futher clarification.

NOTES

Because of the probable composite nature of the genus, the affinities of the three species of Lithosmvlidia are considered separately. It can be said, however, that the genus has a combination of characters suggestive of the Polystoechotidae and/or the Osymlidae, viz. wing medium to large and over  $2 \times$  as long as wide, Sc fused with  $R_1$  and thence curved posteriad, Rs extensively pectinate, MP forked near the base, anal region extensive. However, it also has certain features (which may be preservation artifacts) which do not occur in either family, viz. the apparent absence of subcostal crossveins and, with the exception noted in the generic description above, of  $r_1$ -rs. The genus was originally ascribed by Rick to the Osmylidae Kempyninae, but the analyses which follow show that such a placement is not justified. The basal stem of MA figured by Riek (1955, fig. 22), and given by him as one of the generic characters, is not present in any of the forewing material examined hercin.

# Lithosmylidia lineata Rick (Figs 1,2)

(partim non) Lithosmylidia lineata Rick, 1955, p. 678-9, fig. 22, pl. 3, figs 7-9. [Specimen C1642-3 (pl. 3, fig. 8) = Lithosmylidia sp. A.]

# DESCRIPTION

Forewing. Width (between Sc and posterior margin at CuA): 7.7 mm (C2189-90), 5.7 mm (C867-8): branches of  $Sc + R_1$  long, many deeply forked; Rs with 14 branches (data from C2189-90 only), each forked apically; MA forked apically, similarly to Rs branches;  $MP_1$ and MP, deeply forked, each with 3 main branches; Cu4 deeply forked with 4 (C867-8) or 6 (C2189-90) main branches (in C2189-90 the distal branch is fused for a short length with the proximal branch of  $MP_2$ ; CuP deeply forked, with 3 main branches; 1A (based on C867-8see Fig. 2) ? obliquely pectinate; crossveins not well preserved, but apparently few in number, those detected illustrated in Figs 1,2; nygmata not detected; trichosors not preserved.

### MATERIAL EXAMINED

Holotype UQDG C2189–90 (incomplete forewing), UQDG C867–8 (incomplete forewing), both 'Mount Crosby Insect Bed'. L. lineata must be considered as belonging in, or near to, the Polystoechotidae, based on the following combination of characters (see Table 3): basal stem of MA absent; crossveins of Rs-MA field apparently restricted to two irregular gradate series; CuA obliquely pectinate; CuP deeply dichotomous.

If L. lineata is considered a polystoechotid. then the position of the primary fork of MP does not necessarily indicate that the two specimens are forcwings (one of the unique features of the hindwings of two of the three polystoechotid genera. Polystoechotes Burmeister and Platystoechotes Carpenter, is the lateness of the primary forking of MP - see Carpenter, 1940, figs 69, 71). The very long apical branches of  $MP_2$  and Cu in the two specimens do, however, provide additional evidence that they are indeed forewings (these are much shorter in polystoechotid hindwings).

Specimen C867-8 is considerably smaller than the holotype, but has basically the same vein branching pattern. The fact that CuA has



- FIGS 1, 2. Lithosmylidia lineata; 1, UQDG C2189-90 (holotype); 2, UQDG C867-8.
- Fig. 3. Lithosmylidia baronne, QM F14358 (holotype) (Sc and R are contiguous basally, not fused).

two fewer main branches can be attributed to the smaller wing size. Similar intraspecific variation in size and absolute numbers of vein branches occurs in recent Polystoechotidae. The apparent difference in the number of crossveins cannot be considered significant, as crossveins are so poorly preserved in the material examined.

## Lithosmylidia baronne sp. nov. (Fig. 3)

DESCRIPTION

Forewing. Width (between Sc and posterior margin at CuA): 5.4 mm; costal margin broadly emarginate proximally; costal space quite broad, with crossveins widely spaced. apparently mostly simple, but a few deeply forked; humeral vein upright, simple; Rs with more than 6 branches, the 3rd one forked not far from its base;  $MP_1$  and  $MP_2$  deeply forked,  $MP_2$ with 4 main branches; CuA deeply forked, with 5 main branches, the proximal one extensively subdivided; CuP deeply forked, with 3 main branches,  $CuP_2$  simple; anals widely spaced basally; 1A appearing deeply dichotomously forked (the wing is, however, broken between CuP and 1A and it is possible that 1A is indeed pectinate); 2A forked close to base, the anterior fork with 5 short, simple, obliquely pectinate apical branches, the posterior fork with 4 such branches; 2A and 3A forming a loop basally enclosing 2a-3a; 3A apparently simple; crossveins not well preserved, but apparently few in number, those detected illustrated in Fig. 3; nygmata not detected; trichosors preserved as in Fig. 3.

# MATERIAL EXAMINED

Holotype QM F14358 (incomplete forewing), Gayndah Beds, road cutting c. 3 km ENE Gayndah, central Queensland (collected by K.J. Lambkin, 1975).

### NOTES

This species differs from *L. lineata* in the deep forking of the third *Rs* branch, the extensively subdivided proximal branch of CuA and the simple  $CuP_2$ .

The affinities of the species are problematical. It has the following features which suggest the Polystoechotidae: basal stem MA absent; crossveins of Rs-MA field very limited; CuAobliquely pectinate; CuP deeply dichotomously forked. On the other hand, the humeral vein is simple and not strongly recurrent, 2A is extensively pectinate with the apical branches short and simple, and 3A is simple (see Table 3). Indeed the pectinate form of 2A, the simple nature of 3A, and the fact that these veins form a basal loop enclosing 2a-3a, are somewhat characteristic of the Osmylidae (see Table 2). If these features were considered apomorphous, and those listed above as suggestive of the Polystoechotidae to be generally plesiomorphous, then the species would necessarily be placed closer to the Osmylidae. In summary it may be said that L. baronne is an enigmatic osmylid-like species with a mix of osmylid and polystoechotid characters, as well as some features not occurring in either family (i.c. absence of a subcostal crossvein and  $r_1 - r_3$ ).

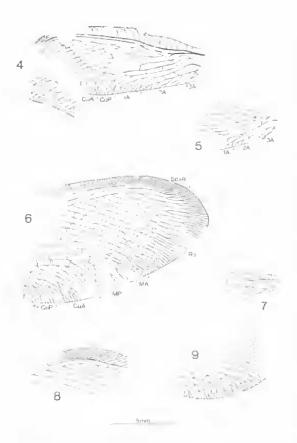
Baronne is the name of the road near Gayndah where the insect bearing shales of the Gayndah Beds are exposed.

### Lithosmylidia parvula Riek (Figs 4, 5)

Lithosmylidia parvula Riek, 1955, p. 679.

#### DESCRIPTION

*Forewing*. Width (between *Sc* and posterior margin at CuA) c. 4.4 mm (QM F14359); posteroapical margin slightly emarginate; costal space quite narrow, with crossveins widely spaced, apparently mostly simple proximally and mostly forked distally; humeral vein slightly recurved, simple;  $Sc + R_1$  field similar to that of L. lineata; specimen C1991-2 with 1 oblique  $r_1$ -rs near 3rd Rs branch,  $r_1$ -rs not detected in other material; Rs with 10 or 12 branches, each forked apically; crossveins of Rs-MA field restricted to a few random ones proximally and 2 irregular gradate series distally; 1m-cu oblique; apical branching of MA and MP not preserved: branches of CuA and CuP markedly shorter and *CuA* apparently more transversely pectinate than in the 2 preceding species; proximal branch only of CuA clearly preserved; *CuP* with 3 main branches; anals widely spaced basally; 1A long, with 6 short, mostly simple, obliquely pectinate branches; 2A long and extensively pectinately forked, with 8 branches, some of these with small marginal forks; 3A and proximal pectinate branch of 2A forming a loop basally enclosing 2a-3a; 3A simple; crossveins of cubital and anal fields as in Fig. 4; 1 nygma detected (in OM F14359 — see Fig. 4), placed near primary fork of MP (because of fragmentation of the specimen in this region the exact position of the nygma is unknown); trichosors



FIGS 4, 5. Lithosmylidia pareula: 4, QM F1459 (Sc and R are contiguous basally, not fused; basal fork of Cu displaced anteriorly); 5, UQDG C1029-30 (holotype) (basal region only).

Fig. 6. Lithosmylidia sp. A, UQDG C1642-3.

Figs 7-9 (rough sketches only). Neuroptera incertae sedis: 7, UQDG C2088-9; 8, UQDG C786-7; 9, UQDG C1039-40.

detected in QM F14359, those preserved illustrated in Fig. 4.

### MATERIAL ENAMINED

Holotype UQDG C1029-30 (indistinctly preserved complete forewing), UQDG C1991-2 (indistinctly preserved almost complete forewing), UQDG C2092-3 (indistinctly preserved incomplete forewing), all 'Mount Crosby Insect Bed'; QM F14359 (fragmented almost complete forewing), Mount Crosby Fossil Insect Locality B (collected by K.J. Lambkin, 1975).

#### NOTES

The above description is based almost entirely on QM F14359. The UQDG specimens are more or less complete but are very indistinctly preserved, and have only contributed information on the form of the  $Sc + R_1$  and the anal fields, and the number of Rs branches. Confirmation of the identity of the QM specimen was made by comparison of its anal field with that of the holotype (Fig. 5).

L. parvula is smaller than the preceding species, the branches of Cu are markedly shorter and CuA is apparently more transversely pectinate. It also differs from L. baronne in having a narrower costal space and in the structure of 2.4.

The affinities of L. purvula are again problematical, but the available material offers a more complete picture of its venation than in the preceding species. Except that CuP is dichotomous rather than pectinate (as it is in all osmylids), the species would, with confidence, be referred to the Osmylidae (see Table 2), albeit showing a unique mix of subfamily characters, viz. crossveins of Rs-MA field limited to a few random ones proximally and two irregular gradate series distally (Protosmylinae only), MP forked close to the base (Protosmylinae, Kempyninae, Spilosmylinae, Gumillinae. Osmylinae), anal field extensive, occupying a considerable part of the posterior margin (Kempyninae, Osmylinae, Stenosmylinae, Eidoporisminae); and having certain features not found in recent Osmylidae, viz. 1m-cu oblique, and the apparent absence of the basal subeostal erossvein, numerous  $r_1$ -rs and the basal stem of M.A. The absence of a clearly pectinate CuP, however, preeludes L. parvula from the Osmylidae, but as in L. baronne, the presumed apomorphous structure of the anal field suggests a sister relationship with that family.

### Lithosmylidia sp. A (Fig. 6)

(partim) Lithosinylidia lineata Riek, 1955, p. 678–9, fig. 33, pl. 3, figs 7–9. [Specimen C1642–3 (pl. 3, fig. 8) non Lithosmylidia lineata Riek].

#### MATERIAL EXAMINED

UQDG C1642-3 (apical half of forewing), "Mount Crosby Insect Bed'.

#### NOTES

This specimen was considered by Riek as the hindwing of *L. lineata*. There are no particular features which indicate that it is a hindwing and indeed the available evidence, tenuous though it is, suggests a forewing. Thus the  $Sc + R_1$  field is

# **RE-EXAMINATION OF LITHOSMYLIDIA**

	Species <sup>2</sup>	Age and Locality	Figured <sup>3</sup>	Family Placement <sup>4</sup>
1.	<i>Epigambria longipennis</i> Handlirsch, 1939	Ju, W. Germany	HN 1939, pl.7, fig.119	Epigambriidae (HN 1939) Nymphitidae (MA 1949, 1962)
2.	<i>Epiosmylus longicornis</i> Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.104	Epiosmylidae (PA 1980)
3.	Gigantotermes excelsus (Hagen, 1862)	Ju, W. Germany	OP 1888, pl.30, fig. 1 (as <i>Apochrysa excelsa)</i> HN 1907, pl.48, fig 11	Nymphitidae (HN 1906) Neuroptera <i>i.s.</i> (MA 1949) Hemerobiidea <i>i.s.</i> (MA 196
4.	Grammosmylus acuminatus Panfilov, 1980	Ju, U.S.S.R	PA 1980, fig.105	Grammosmylidae (PA 1980
5.	Ineptiae meunieri Handlirsch, 1906	Ju, W. Germany	-	Neuroptera <i>i.s.</i> (HN 1906; MA 1949) Hemerobiidae <i>i.s.</i> (MA 196
6.	Kasachstania fasciata Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.97	Osmylidae (PA 1980)
7.	Kirgisellodes ornatus (Martynov, 1925)	Ju, U.S.S.R.	MV 1925, fig.11 MA 1962, fig.859	Prohemerobiidae (MV 192: Osmylitidae (MA 1949, 1962)
	Lithosmylidia lineata Riek, 1955	Tr, Australia	Figs 1,2	discussed herein
).	L. parvula Riek, 1955	Tr, Australia	Figs 4,5	discussed herein
).	L. baronne sp.nov.	Tr, Australia	Fig.3	discussed herein
	<i>Loxophleps costalis</i> Handlirsch, 1939	Ju, E. Germany	HN 1939, pl.6, fig.111	Solenoptilidae (HN 1939) Neuroptera <i>i.s.</i> (MA 1949) Hemerobiidea <i>i.s.</i> (MA 196
2.	<i>Melamnous indistinctus</i> Handlirsch, 1939	Ju, E. Germany	HN 1939, pl.7, fig.117	as 11.
3.	Melaneimon dubium Handlirsch, 1939	Ju, E. Germany	HN 1939, pl.7, fig.120	as 11.
1.	Mesonymphes hageni Carpenter, 1929	Ju, W. Germany	CA 1929, fig.1	Nymphitidae (CA 1929; M 1949, 1962)
5.	<i>M. rohdendorfi</i> Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.115	Nymphidae (PA 1980)
5.	Mesopolystoechus apicalis Martynov, 1937	Ju, U.S.S.R.	MV 1937, fig.18 MA 1949, fig.8 MA 1962, fig.860	Prohemerobiidae (MV 193 Mesopolysteochotidae (MA 1949, 1962)
7.	Mesosmylina exornata Bode, 1953	Ju, W. Germany	BO 1953, fīg.320	Prohemerobiidae Mesosmylinae (BO 1953) Osmylitidae (MA 1962)
8.	M. mongolica Ponomarenko, 1984	Ju, Mongolia	PO 1984, fig.1	Osmylidae (PO 1984)

TABLE 1. Mesozoic 'osmylid-like' fossil Neuroptera<sup>1</sup>

TABLE 1. (continued)

	Species <sup>2</sup>	Age and Locality	Figured <sup>3</sup>	Family Placement <sup>4</sup>
19.	M. sibirica Ponomarenko, 1985	Ju, U.S.S.R.	PO 1985, fig.5	Osmylidae (PO 1985)
20.	Mesosmylus atalantus Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.103	Osmylidae (PA 1980)
21.	Microsmylus foliformis Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.114	Mesochrysopidae (PA 1980)
22.	Minonymphites orthophlebes Hong, 1980	Tr, China	HO 1980, fig.16	Nymphitidae (HO 1980)
23.	Nymphites priscus (Weyenbergh, 1869)	Ju, W. Germany	WY 1869, pl.34, figs 13,14 (as <i>Hemerobius</i> priscus)	Nymphitidae (HN 1906; MA 1949, 1962)
24.	N. braueri Haase, 1890	Ju, W. Germany	HS 1890, pl.1, fig.11 HN 1907, pl.48, fig.9	as 23.
25.	N. lithographicus Handlirsch, 1906	Ju, W. Germany	-	as 23.
26.	<i>Osmyliodea distinctus</i> Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.101	Osmylidae (PA 1980)
27.	Osmylites protogaeus (Hagen, 1862)	Ju, W. Germany	OP 1888, pl.30, fig.2 (as <i>Chrysopa excelsa</i> ) HS 1890, pl.1, fig.10 (as <i>Osmylites protogaea</i> ) HN 1907, pl.48, fig.4	Prohemerobidae (HN 1906) Epigambriidae (HN 1939) Osmylitidae (MA 1949, 1962)
28.	<i>Osmylopsis duplicata</i> (Giebel, 1856)	Ju, England	WS 1854, pl.18, fig.42 (as 'orthopterous wing') HN 1907, pl.48, fig.15	Neuroptera <i>i.s.</i> (HN 1906; MA 1949) Epigambriidae (HN 1939) Hemerobiidea <i>i.s.</i> (MA 1962)
29.	Palaeoleon ferrogeneticus Rice, 1969	Cr, Canada	RI 1969, figs 2,3	Myrmeleontidae (RI 1969)
30.	Palparites deichmulleri Handlirsch, 1906	Ju, W. Germany	-	Neuroptera <i>i.s.</i> (HN 1906; MA 1949) Hemerobiidea <i>i.s.</i> (MA 1962)
31.	Parosmylus latus Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig. 102	Osmylidae (PA 1980)
32.	Petrushevskia borisi Martynova, 1958	Tr, U.S.S.R.	MA 1958, fig.8 MA 1962, fig.858	Osmylitidae (MA 1958 1962)
33.	Pronymphites elegans Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.99	Osmylidae (PA 1980)
34.	Pterocalla superba Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.100	as 33.
35.	Scapoptera recta Panfilov, 1980	Ju, U.S.S.R.	PA 1980, fig.98	as 33.

TABLE 1. (continued)

	Spccies <sup>2</sup>	Age and Locality	Figured <sup>3</sup>	Family Placement <sup>4</sup>
36.	Sialium sipylus Westwood, 1854	Ju, England	WS 1854, pl.18, fig.24 HN 1907, pl.48, fig.10	Nymphiiidae (HN 1906; MA 1949, 1962)
37.	Sibosmylina libelluloides Ponomarenko, 1985	Ju, U.S.S.R.	PO 1985, fig.6	Osmylidae (PO 1985)
38.	Sogjuta speciosa Martynova, 1958	Tr, U.S.S.R.	MA 1958, fig.9 MA 1962, fig.853	Nymphitidae (MA 1958. 1962) Osmylidae (AD 1969)
39.	Solenoptilon kochi (Gcinitz, 1887)	Ju, E. Germany	HN 1907, pl.41 fig.84	Solcnoptilidae (HN 1906. 1939; MA 1949, 1962)
40.	S. martynovi Martynova, 1949	Ju. U.S.S.R.	MA 1949. fig.6 MA 1962. fig.852	Solenoptilidae (MA 1949, 1962)
41.	Tetanoptilon brunsvicense Bode, 1953	Ju, W. Germany	BO 1953, pl.13, fig.344	Solenoptilidae (BO 1953) Osmylitidae (MA 1962)

Abbreviations: AD = Adams, BO = Bode, Cr = Cretaccous, CA = Carpenter, HS = Haase, HN = Handlirsch, HO = Hong, Ju = Jurassic, MC = MacLeod, MV = Martynov, MA = Martynova, OP = Oppenheim, PA = Panfilov, PO = Ponomarenko, RI = Rice, Tr = Triassic, WS = Westwood, WY = Weyenbergh, *i.s. = incertae* sedis.

<sup>2</sup> For the sake of convenience I have accepted Handlirsch's nomenclature of the 19th century species, even though the validity of some appears doubtful.

<sup>3</sup> Line drawings only included.

4 20th century references only.

no more narrow than in the holotype forewing of L. lineata (in both Osmylidae and Polystoechotidae, the  $Sc + R_1$  field of the hindwing is invariable narrower than that of the forewing),  $Sc + R_1$  does not extend as far around the apical margin as in the holotype forewing of L. lineata (in most Osmylidae  $Sc + R_1$  in the hindwing extends slightly further around the wing margin towards the apex than in the forewing), and the branches of CuA are long (in the hindwing of the Polystoechotidae they are much shorter).

C1642-3 is similar in size and basic features to L. lineata, but differs in the much more deeply forked MA and branches of Rs and also in the apparently more extensively forked proximal branch of Cu.4, although this latter feature is uncertain owing to the doubtful identity of the veins in this region of the wing. Because of the difference in the form of the Rs branches and MA, C1642-3 cannot be considered as conspecific with L. lineata. Intraspecific variation of this extent does not occur in recent Neuroptera. The specimen is too incomplete to be named and is thus here designated L. sp. A.

The crossveins in the specimen are not well preserved and Fig. 6 shows all that were detected. Trichosors are present but not clearly preserved.

## Neuroptera incertae sedis (Figs 7-9)

Riek mentioned three further specimens from Mount Crosby (UQDG C2088–9, C786–7, C1039–40) in his descriptions of *Lithosmylidia* and referred these 'very doubtfully' or 'doubtfully' to *L. lineata* or *L. parvula*. The three specimens are all very fragmentary, as indicated by Rick, and until more clearly and completely preserved material of the *Lithosmylidia* species becomes available for exact comparison, they can be referred to as no more than Neuroptera **TABLE 2.** Distinguishing features of the wings of Osmylidae

- 1. Trichosors present.
- 2. Membrane with microtrichia, including a modified area behind 3A (see Riek 1966).
- 3. Nygmata present.
- 4. Jugal lobe present.
- 5.  $Sc + R_1$  entering margin well before wing apex, with branches short and usually mostly simple (apical field of wing thus occupied mostly by *Rs*).
- 6. Numerous  $r_1$ - $r_s$ .
- 7. Rs-MA field with a few to very numerous randomly placed crossveins proximally and 1 or 2 irregular gradate series distally; random crossveins not extending beyond level of point of fusion of Sc and  $R_1$  (except in Gumilla Navás and Porismus McLachlan).

### Forewing:

- 8. Humeral vein simple, at most only slightly recurrent.
- 9. 1 only (basal) subcostal crossvein (except *Porismus* which has numerous additional ones).
- Origin of *Rs* close to base of wing; without presectoral veins (excluding basal stem of *MA*).
- 11. 1*m*-*cu* and basal stem of *MA* usually, but not always, aligned; these veins upright or slightly oblique.
- 12. *MP* always forked, but fork variably placed, ranging from near the base (e.g. Protosmylinae) to near the margin (e.g. most Stenosmylinae).
- Without 'oblique vein' (between MP and CuA — see Tillyard 1916).
- 14. At least CuP, and often CuA as well, pectinate, with branches more or less transverse.
- 15. CuP not fused with 1A.
- 16. Anal field variable, but sometimes (e.g. Kempyninae, Stenosmylinae) quite extensive, reaching to c. 0.3–0.4 wing length and thus occupying a considerable part of the posterior margin.
- 17. Anals widely spaced basally; 1*A*. and 2*A* of variable extent, but always clearly pectinate, with branches short and usually simple; 3*A* quite long, but not deeply forked; 2*A* and 3*A* often forming a loop basally, enclosing 2a-3a.
- 18. Basal 1a-2a clearly distal to basal 2a-3a.

### Hindwing:

- 19. Subcostal crossveins as in forewing.
- 20. Origin of *Rs* close to wing base; without presectoral veins.
- 21. Stem of MA often present.
- 22. *MP* forked very close to base, at or before origin at *Rs*.

- 22. *MP* forked very close to base, at or before origin at *Rs*.
- 23. At least CuA, and often  $MP_2$  as well, pectinate.
- 24. CuA extending to at least 1/2 wing length.
- 25. Base of *CuP* not developed as an upright cubital brace.
- 26. CuP not fused with 1A.
- 27. CuP, when multibranched, pectinate.
- 28. Anal field of small but variable extent; 1*A* and 2*A* pectinate, 1*A* with 2–8 branches; 3*A* quite long, not deeply forked, distinctly angulate at 2a-3a.

incertae sedis. C2088–9 (Fig. 7) is a clearly preserved hindwing fragment which shows the very narrow costal space characteristic of hindwings, simple costal crossveins, the base of Rs, Rspectinately branched, two clear  $r_1$ -rs, and most interestingly a nearly longitudinal basal stem of MA. C786–7 (Fig. 8) preserves the anterior apical region of a fore- or hindwing of similar size to that of the holotype of L. lineata, and shows the  $Sc + R_1$  field (similar to that of L. lineata), Rs pectinately branched, a single crossvein between  $Sc + R_1$  and Rs, and trichosors. C1039–40 (Fig. 9) preserves the apical posterior margin of a fore- or hingwing and shows the apical branches of (?) MA, MP and CuA.

# NOTES ON MESOZOIC 'OSMYLID-LIKE' FOSSIL NEUROPTERA

*Lithosmylidia* falls into a group of Mesozoic fossil neuropterous wings which, for the sake of discussion, are herein referred to as 'osmylid-like', and have the following features:

- 1. wing of medium to large size, at least  $2 \times$  as long as wide,
- 2. Sc and  $R_1$  fused apically and thence curved posteriad,
- 3. *Rs* with numerous pectinate branches running towards the posteroapical margin.

This suite of very basic features is characteristic of the modern families Osmylidae, Polystoechotidae, Nymphidae and Myrmeleontidae, but several of these Mesozoic 'osmylid-like' wings demonstrate to varying degrees the characteristics of the Chrysopidae

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TABLE 3. Distinguishing features of the wings of Polystocchotidae

- 1. Trichosors present.
- 2 Membrane without microtrichia, except for a modified area behind 3.4. (see Riek 1966).
- 3. Nygmata present.
- 4. Jugal tobe present.
- 5.  $Sc + R_1$  (*Polystoechotes*), or  $R_1$  (not fused with Sc) (*Platystoechotes*, *Fontecilla*), entering margin near or before wing apex, with branches long and mostly forked.
- 6. Few  $r_1$ -rs (2-9 in material examined).
- 7. Crossveins of *Rs-MA* field restricted to 1 or 2 irregular gradate series (no crossveins proximally).
- Forewing:
- Humeral vein strongly recurrent, with numerous forked branches.
- 9. 1 only (basal) subcostal crossvein.
- Origin of Rs close to base of wing; without presectoral veins.
- 11. Basal stem of MA absent; tm-cu oblique.
- 12. MP forked at c. ¼ length
- 13. Without 'oblique vein'.
- 14. *MP*<sub>2</sub> and *CuA* deeply pectinate, with branches strongly oblique; *CuP* deeply dichotomous.
- 15. CuP not fused with 1A.
- Anal field occupying an extensive area of base of wing, extending to c. 0.3 wing length.
- Anals widely spaced basally; 1A dccply dichotomous (Polystoechotes, Platystoechotes), or primitively pectinate (i.e. with branches long, oblique and deeply dichotomously forked) (Fontecilla); 2A dceply dichotomous (Polystoechotes), or rending to pectination (Platystoechotes, Fontecilla); 3A long, deeply dichotomously forked; 2A and 3A not forming a loop basally.
- 18. 1a-2a clearly distal to 2a-3a.

#### Hindwing:

- 19. Subcostal space without crossveins.
- Origin of Rs close to wing base; without presectoral veins.
- 21. Stem of M.4 present.
- MP forked close to base, before (Fontecilla) or after (Polystoechotes, Platystoechotes) origin of Rs.
- 23.  $MP_2$  few branched, weakly pectinate; Cu.4 pectinate, with branches oblique.
- 24. Cu.4 extending to at least 1/2 wing length.
- Base of CuP not developed as an upright cubital brace.
- 26. CuP not fused with 1.4.
- 27. CuP deeply dichotomous.
- 28. Anal field fairly extensive; 1.4 and 2.4 as in forewing, but with 1.4 in *Fontecilla* more obviously pectinate; 3.4 long and deeply forked, not angulate at 2a-3a.

(see Adams, 1967), and have probably correctly been ascribed to the Mesochrysopidae - the family of Mesozoic chrysopid or near-chrysopid forms (Adams, 1985). Included in this latter group are the following Jurassic 'osmylid-like' species which will not be discussed further herein: Mesochrysopa zitteli (Meunier, 1898) 1907. (Handlirsch, pl\_ 48. fig. 14). Aristenymphes perfectus Panfilov, 1980, (Panfilov, 1980, fig. 108), Chrysoleonites ocellatus Martynov, 1925, (Martynov, 1925, fig. 10; Martynovoa, 1949, figs 4, 5, 1962, fig. 854), C. intactus Panfilov, 1980, (Panfilov, 1980, lig. 106), C. plexus Panfilov, 1980, (Panfilov, 1980, fig. 107), Macronymphy elegans Panfilov, 1980, (Panvilov, 1980, fig. 110). Nymphoides latus Panfilov, 1980, (Panfilov, 1980, fig. 109), N. udensis Ponomarenko, 1984, (Ponomarenko, 1984, fig. 7), Mesotermes heros (Hagen, 1862) (Hagen, 1862, pl. 15, fig. 1 – as *Termes heros*) and Pseudomyrmeleon extinctus (Weyenbergh, 1869) (Weyenbergh, 1869, pl. 35, figs 16, 16aas *Myrmeleon extinctus*). The latter two species are very poorly known and are included here only on the basis of Handlirsch's (1906, p. 613-4) assessment.

Of the remaining 'osmylid-like' wings several can be placed with some confidence in one or other of the Osmylidae, Polystoechotidae. Nymphidae or Myrmeleontidae, while others, although not showing features absolutely characteristic of one of these families, can be discussed in terms of showing more similarity to one or two rather than others. Table 1 lists alphabetically these 'osmylid-like' species and includes all Mesozoic fossil Neuroptera with the three characters listed above (excluding those ascribed to the Mesochrysopidae), as well as any others which have been included in the Osmylitidae, Nymphitidae and Mesopolystoechotidae, the families erected to include Mesozoic forms with affinities to the three modern families nominally alluded to. Of the 41 species listed three groups are excluded from further discussion for the following reasons:

Group 1: Egigambria longipennis, Gigantotermes excelsus, Kirgisellodes ornatus, Nymphites priscus, N. braueri, Osinyhtes protogaeus, Osnivlopsis duplicata, Pronymphites **TABLE 4.** Distinguishing features of wings of Nymphidae.

- Trichosors present.
   Membrane without microtrichia (except Nesydrion Gerstaecker — see Riek 1966).
- 3. Nygmata absent.
- 4. Jugal lobe absent.
- 5.  $Sc + R_1$  entering margin at or beyond wing apex, with branches long and mostly forked  $(Sc + R_1$  thus occupy a major part of the apical field).
- 6. Numerous  $r_1$ -rs.
- 7. *Rs*-*MA* field with numerous randomly placed crossveins extending beyond level of point of fusion of *Sc* and *R*<sub>1</sub>.
- 7a. MA never extensively forked.

#### Forewing:

- 8. Humeral vein simple, at most only slightly recurrent.
- 9. At least 1 (basal) subcostal crossvein, and often with numerous additional ones.
- 10. Origin of Rs close to base of wing; without presectoral veins (excluding basal stem of MA).
- 11. *Im-cu* and basal stem of *MA* aligned, and upright or slightly oblique.
- 12. *MP* forked between <sup>1</sup>/<sub>4</sub> and <sup>1</sup>/<sub>2</sub> length, or simple.
- 13. Without 'oblique vein'.
- 14. At least CuP, and usually CuA as well, pectinate (CuA sometimes forming a large triangular area as in the Myrmeleontidae).
- 15. CuP not fused with 1A.
- 16. Anal field small, occupying a limited area extending, at most, to *c*. 0.2 wing length.
- 17. Anals closely spaced basally; 1A and 2A short, when multibranched, pectinate; 3A short, not deeply forked; 2A and 3A not forming a loop basally (except a very large one in *Austronymphes* Esben-Petersen).
- 18. Basal 1a-2a aligned with, or slightly proximal to, basal 2a-3a.

### Hindwing:

- 19. One (basal) subcostal crossvein, or without basal one but with numerous others.
- 20. Origin of *Rs* either close to wing base (without presectoral veins), or more distally placed (with several presectorals).
- 21. Stem of MA absent.
- 22. *MP* forked very close to base, before origin of *Rs*.
- 23.  $MP_2$  and CuA pectinate.
- 24.  $Cu\bar{A}$  of variable extent, but usually not reaching beyond  $\frac{1}{2}$  wing length.
- 25. Base of *CuP* developed as an upright cubital brace.
- 26. *CuP* and 1A fused in region of cubital brace, but separate distally.
- 27. CuP, when multibranched, pectinate.

28. Anal field occupying a very limited area at base of wing; 1*A* with, at most, 3 branches; 3*A* short, not deeply forked, not angulate at 2*a*-3*a* (except in *Austronymphes* where a large loop is formed similar to the forewing).

*elegans* and *Sialium sipylus* are all based on fairly complete and mostly well preserved wings, but unfortunately the available illustrations (see Table 1) are not accurate enough to allow any new discussion. Their reassessment must await a re-examination of their type-specimens.

Group 2: Loxophleps costalis, Melamnous indistinctus, Melaneimon dubium, Mesosmylina sibirica, Microsmylus foliformis, Parosmylus latus, Scapoptera recta, Solenoptilon kochi and S. martynovi are all based on fragmentary specimens which are not worth further consideration and for the most part should never have been named in the first place. S. kochi and S. martynovi are included in the list on the basis of wing shape and venational facies, even though both are figured with Sc not fused with  $R_1$ . L. costalis and M. dubium are listed because of their placement by Handlirsch (1939) with Solenoptilon in the family Solenoptilidae.

Group 3: Ineptiae meunieri, Nymphites lithographicus and Palparites deichmulleri are all poorly preserved and have never been illustrated with a line drawing. Any reassessment would require re-examination of their types. I. *meunieri* is included because of Handlirsch's (1906, p. 614) opinion that it was 'wahrscheinlich in die Nähe von Gigantotermes' (Table 1: 3), and P. deichmulleri because of Deichmüller's original observation (noted in Handlirsh, 1906, p. 614) that is was similar to Palpares Rambur (Myrmeleontidae).

The 20 remaining species are sufficiently well preserved and illustrated to be discussed with respect to the major distinguishing features of the wings of modern Osmylidae, Polystoechotidae, Nymphidae and Myrmeleontidae as given in Tables 2–5.

Epiosmylus longicornis is not well illustrated but has  $Sc + R_1$  entering the margin before the wing apex, with branches short and simple, and CuP of the forewing extensively tranversely pectinate, and is thus almost certainly an osmylid. The extremely elongate antennae and extensive crossvein network are reminiscent of

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the subfamily Gumillinae [one species only, *Gumilla longicornis* (Walker) — see Adams, 1977], although the branching of MP in the forewing secms to differ considerably (compare Panfilov 1980, fig. 104 with Navás, 1912, fig. 24).

Grammosmylus acuminatus is an enigmatic forewing remarkable for its extremely dense crossvein network. Its basic venational features are: Sc and  $R_1$  fused apically but not curved posteriad; Rs arising close to wing base, with numerous pectinate branches; MA forked at about  $\frac{1}{2}$  length; MP forked near the base; CuA and CuP obliquely pectinately forked, CuA excessively so; anal field extensive. The affinities of G. acuminatus are problematic but it probably warrants the separate family status proposed by Panfilov.

Kasachstania fasciata has short, thick antennae and a forewing with few  $r_1$ - $r_s$ , limited crossveins in the  $R_s$ -MA field,  $MP_2$  and CuAobliquely pectinately forked, CuP deeply dichotomously forked, anal field extensive and 1A apparently pectinately forked. This combination of characters is compatible with the Polystoechotidae, although 1A appears to be more clearly pectinate than in *Fontecilla* Navás (see Table 3).

Lithosmylidia lineata, L. parvula and L. baronne have been discussed in detail herein.

Mesonymphes hageni has the following combination of characters which place it clearly in the Nymphidae:  $Sc + R_1$  entering margin well beyond wing apex, with branches long and deeply forked ( $Sc + R_1$  thus occupying a major part of the apical field); several subcostal crossveins; forewing with origin of Rs close to wing base, without presectoral veins; MP forked near the base; hindwing with base of CuP developed as an upright cubital brace (Phillip Adams, pers. comm.; not illustrated by Carpenter, 1929). Mesonymphes rohdendorfi is a hindwing similar to that of M. hageni, although apparently without subcostal crossveins. The two species are almost certainly congeneric.

Mesopolystoechotes apicalis is better known from the specimen figured by Martynova (1949, 1962) rather than the fragmentary one in Martynov (1937). The Martynova specimen is the apical half of a polystoechotid hindwing with venation not all that dissimilar to that of the modern *Polystoechotes* (compare Martynova, 1949, fig. 8 with Carpenter, 1940, fig. 69). If this assessment is accurate, the venational interpret**TABLE 5.** Distinguishing features of the wings ofMyrmeleontidae

1. Trichosors absent.

- 2. Membrane without microtrichia.
- 3–7. As in Nymphidae.
- 7a. *MA* sometimes extensively dichotomously forked.

#### Forewing:

- 8. Humeral vein simple, not recurrent.
- 9. Subcostal space without crossveins.
- 10. Origin of *Rs* remote from base of wing; at least 2 presectoral veins.
- 11. 1*m*-*cu* and basal stem of *MA* aligned and strongly oblique.
- 12. MP simple.
- 13. 'Oblique vein' usually obvious.
- 14. CuP or CuP + 1A pectinate;  $CuA_1$  and  $CuA_2$ enclosing a large triangular area, apparently formed basically of pectinate branches of  $CuA_1$ , but often developed as a complex network of cells.
- 15. *CuP* nearly always (except e.g. Stilbopteryginae, *Palpares, Pseudimares* Kimmins) fused with 1*A*.
- 16. As in Nymphidae.
- 17. As in Nymphidae.
- 18. Basal 1a-2a and basal 2a-3, when present, variably placed relative to each other.

Hindwing:

- 19. Subcostal space without crossveins.
- 20. Origin of *Rs* remote from wing base; at least 1 presectoral vein.
- 21. Stem of MA abscnt.
- 22. *MP* forked very close to base, before origin of *Rs*.
- 23.  $MP_2$  extensively pectinate or forming a triangular area similar to CuA in forewing; CuA pectinate.
- 24. CuA short, not reaching 1/2 wing length.
- 25. Base of *CuP* developed as an upright cubital brace.
- 26. CuP fused with 1A from cubital brace to margin.
- 27. CuP + 1A, when multibranched, pectinate.
- 28. Anal field occupying a very limited area of base of wing; 2A and 3A nearly always simple (1A fused with CuP); 3A short, not deeply forked, not angulate.

ation of Martynova (1949) rather than Marytnova (1962) is correct.

Mesosmylina exornata is considered an osmylid forewing on the basis of the following combination of characters:  $Sc + R_1$  entering margin well before wing apex, with branches

short and apparently simple; CuP transversely pectinate; anal field extensive, with anals widely spaced basally and 1A long, with numerous short, simple pectinate branches. The crossvein field, as figured by Bode, shows some unusual features e.g. numerous subcostal crossveins, one presectoral vein (excluding basal MA stcm), numerous random crossveins in Rs-MA field beyond level of point of fusion of Sc and R<sub>1</sub>, but these must be treated with caution following Willmann's recent (1984) findings on the accuracy of Bode's descriptions and figures, especially the generous inclusion of numerous non-existent crossveins in his figures.

Mesosmylina mongolica is based on a forewing, reasonably complete but unfortunately critical areas of the base and apex are not preserved. It has the following features which I think are sufficient to place it in the Osmylidae:  $Sc + R_1$  field, although not completely preserved, with branches short and mostly simple; *CuP* pectinate, although with only 4 marginal branches: 1A apparently long, with numerous short, simple pectinate branches. CuA and CuP of M. mongolica differ considerably from those of *M. exornata* and the two species are probably not congeneric.

Mesosmylus atalantus known from the forewing, a fragment of the hindwing and part of the abdomen, is poorly illustrated, even though the specimen itself (Panfilov, 1980, pl. 12, fig. 3) looks good. The forewing is probably that of an osmylid ( $Sc + R_1$  entering margin well before wing apex, with branches short and simple; Rs-MA field with a few random crossveins proximally and two irregular gradate series distally — as in the Protosmylinae; 1A long, apparently with numerous short, simple pectinate branches), although the form of CuP, which appears to have only four marginal branches, is not clearly indicated. The venation of this species appears to be fairly similar to that of Lithosmylidia parvula.

Minonymphites orthophlebes is known from a forewing which, although placed by Hong in the Nymphitidae, does not belong with the other species discussed herein as 'osmylid-like', and is included in this listing only for the sake of completeness. Its affinities are problematical to say the least. The only thing in common with the 'osmylid-like' species is the fact that Sc and  $R_1$ are fused apically and thence curved posteriad, otherwise it has the following combination of features which may even preclude it from the Neuroptera; no end-twigging on any veins; R apparently fused with Sc basally; apical branches of Rs merging with  $Sc + R_1$ ; CuP and anals simple.

Osmyliodea distinctus is known from the apical half of probably a hindwing with the following features, on the basis of which it can be assigned to the Polystoechotidae:  $Sc + R_1$  with branches quite long and forked; few  $r_1$ -rs; crossveins of Rs-MA field few in number and restricted for the most part to one irregular gradate series; CuA obliquely poctinate as in Polystoechotcs; CuP apparently deeply dichotomously forked.

Palaeoleon ferrogeneticus is known from the apical half of a fore- or hindwing which, on the basis of the following combination of characters, is almost certainly a myrmeleontid:  $Sc + R_1$  entering margin well beyond wind apex, with branches long and deeply forkcd ( $Sc + R_1$  thus a major component of the apical field); *MA* deeply and extensively dichotomously forked; *MP* (if a forewing) simple; *CuA* (if a forewing) or *MP*<sub>2</sub> (if a hindwing) extensively pectinate. Ricc's figure (1969, fig. 2) is incorrectly labelled; thus his 'R<sub>2</sub>, R<sub>2a</sub>, R<sub>3</sub>, R<sub>4</sub>, R<sub>5</sub>, M<sub>1</sub>' = *Rs*. 'M<sub>2</sub>, M<sub>3</sub>, M<sub>4</sub>' = *MA*, if the specimen is a forewing 'Cu<sub>1</sub>' = *MP* and 'Cu<sub>2</sub>' = distal section of *CuA*, if a hindwing 'Cu<sub>1</sub>' = *MP*<sub>1</sub> and 'Cu<sub>2</sub>' = distal section of *MP*<sub>2</sub>.

Petrushevskia borisi is a very well preserved forcwing with:  $Sc + R_1$  entering margin well before wing apex; numerous  $r_1$ -rs; random crossveins of Rs-MA field not extended beyond level of point of fusion of Sc and  $R_1$ ; 1m-cu and basal stem of MA not aligned; CuP extensively pectinate; basal 1a-2a clearly distal to basal 2a-3a; anals widely spaced basally, 1A and 2Along and pectinate, with branches short and mostly simple, 2A and 3A forming a loop basally. On the basis of the above combination of characters P. borisi is assigned to the Osmylidae, even though the basal stem MA is more oblique than in recent species.

*Pterocalla superba* is considered a polystoechotid forewing on the basis of the following combination of characters: limited  $r_1$ -rs; Rs-MA field apparently with very few crossveins;  $MP_2$  and CuA deeply pectinate, with branches strongly oblique; CuP and 1A deeply dichotomously forked; 2A apparently obliquely pectinate.

Sibosmylina libelluloides, although included by Ponomarenko (1985) in Panfilov's (1980) expanded Osmylidae, does not belong in this 'osmylid-like' group of species or probably even in the Neuroptera. It is included herein for the sake of completeness only.

Sogjuta speciosa is known from a nearly complete forewing with:  $Sc + R_1$  entering margin well before wing apex, with branches short and mostly simple; Rs-MA field with two crossveins proximally and two irregular gradate series distally; CuP pectinate; anals widely spaced basally, 1A pectinate, with branches short. On the basis of these features S. speciosa is considered an osmylid, even though it has only six  $r_1-rs$ .

Tetanoptilon brunsvicense, although poorly illustrated (see notes under Mesosmylina exormata), is considered a forewing on the basis of the broad separation at the base of the veins labelled 'Cu' and 'A' by Bode. If it was a hindwing as suggested by the narrow costal space, these veins would have to be Cu.4 and CuP respectively, and thus have a common stem. If this venational interpretation is correct, T brunsvicense must be considered an osmylid, with CuP transversely pectinate and the anal field extensive with 1A very long, with numerous short, simple pectinate branches.

In summary, the 20 'osmylid-like' or supposed 'osmylid-like' species on which comment can be made can be classified into seven categories:

- Species not 'osmylid-like' and possibly not even neuropterous: Minonymphites orthophlebes, Sibosmylina libelluloides.
- 2. Neuroptera of problematical alfinities: Grammosmylus acuminatus (Grammosmylidae).
- Species similar to Osmylidae or Polystoechotidae, but not able to be placed in either: Lithosmylidia baronne, L. parvula.
- 4. Probable Osmylidae: Epiosmylus longicornis, Mesosmylina exornata, M. mongolica, Mesosmylus atalantus, Petrushevskia borisi, Sogjuta speciosa, Tetanoptilon brunsvicense,
- 5. Probable Polystoechotidae: Kasachstania fasciata, Lithosmylidia lineata, Mesopolystoechotes apicalis, Osmyliodea distinctus, Pterocalla superba.
- Probable Nymphidae: Mesonymphes hageni, M. rohdendorfi.
- 7. Probable Myrmeleontidae: Palaeoleon ferrogeneticus.

Little comment can be made concerning the status of the families Osmylitidae, Nymphitidae and Mesopolystoechotidae while so many important species, including those of the typegenera of Osmylitidae and Nymphitidae, remain so poorly known.

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